

NEW SPECIES OF ALVINELLIDAE (POLYCHAETA) FROM THE NORTH FIJI BACK-ARC BASIN HYDROTHERMAL VENTS (SOUTHWESTERN PACIFIC)

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Abstract. — The polychaete family Alvinellidae Desbruyères & Laubier, 1986 comprises two genera, *Alvinella* and *Paralvinella*, and ten species or subspecies. All species are strictly associated with hydrothermal vents in the Pacific Ocean. The genus *Paralvinella* includes eight species or sub-species, plus one additional new species presently being described from North East Pacific hydrothermal fields. In 1989, the French research submersible *Nautilie* had 12 successful dives in the North Fiji back-arc Basin and explored two active hydrothermal vents. Numerous specimens of two additional new species of the genus *Paralvinella* were collected using the manipulator of the submersible. *Paralvinella unidentata*, new species, exhibits several features that lead us to erect three different subgenera, *Paralvinella* s. s., *Miralvinella*, new subgenus and *Nautalvinella*, new subgenus, within the genus *Paralvinella*. This species lives within the anhydrite mass, very close to hot fluid openings. The second new species, *P. fijiensis*, found in the anhydrite mass, but also on basaltic rocks, is closely related to *P. grasslei*, the type species, and to *P. palmiformis*.

While the first discovery of hydrothermal phenomena occurring at the axes of oceanic ridges goes back to 1976 (Lonsdale 1977), the exploration of hydrothermal systems in back-arc basins is rather recent (Both et al. 1986, in Manus Basin, Hessler et al. 1988, in Marianas back-arc Basin, Fouquet et al. 1990, 1991, in Lau Basin, Ohta 1990, in Okinawa back-arc Basin) (Auzende et al. 1989, Jollivet et al. 1989). During the early summer of 1989, a French-Japanese biological cruise, STARMER 2 (30 June 1989 to 19 July 1989) was devoted to the study of biological communities associated with deep-sea hydrothermal vents in the Southwestern Pacific, in the North Fiji back-arc Basin (Desbruyères et al. 1991). The French research submersible *Nautilie*, operated from R/V *Le Nadir*, had 12 successful dives in these areas. Two different active sites were explored. White Lady vent has one large diffuser plus several small cylindrical chimneys; the edifice is a few meters high and is

built up by anhydrite, with hydrothermal fluid temperature up to 285°C; the fluid is translucent, relatively depleted of metal due to subsurface phase separation and shows a low content of hydrogen sulfide. The site is located at a depth of 2000 m at 16°59'S and 173°55'E. Another hydrothermal field named Mussel Valley consists of *Bathymodiolus* spp. beds developing on the basalt; there is no chimney and the hydrothermal fluid diffuses from cracks between basaltic rocks; the fluid temperature does not exceed 8.5°C. This site is located at a depth of 2700 m at 18°49'S and 173°29'E. A large collection of polychaetes including representatives of the family Alvinellidae were collected from the submersible.

Since our last publication on Alvinellidae (Desbruyères & Laubier 1991), the total number of known *Paralvinella* species includes eight species or subspecies (Detinova 1988). At least one additional new species from North East Pacific hydrothermal fields

is presently being described and additional material tentatively identified as *Paralvinella hessleri* has recently been collected from Okinawa vent fields (Miura & Ohta 1991).

During the dives in the North Fiji Basin, numerous specimens of two different species of the genus *Paralvinella* were collected using the manipulator of the submersible. Morphological study of these animals showed that they represent two new species, *Paralvinella unidentata* and *P. fijiensis*. *Paralvinella unidentata* exhibits several features that lead us to erect three different subgenera within the genus *Paralvinella*. This species lives in the anhydrite mass, very close to hot fluid openings. The second new species, *Paralvinella fijiensis*, found in the anhydrite mass and on basaltic rocks, is closely related to *P. grasslei*, the type species, and *P. palmiformis*.

Paralvinella unidentata, new species

Figs. 1, 3, 4

Type locality, material examined.—Seventy-eight specimens collected during *Nautile* dives PL 10 (3 specimens, White Lady site), PL 11 (5 specimens, White Lady site), PL 16 (37 specimens, White Lady site), PL 20 (32 specimens, White Lady site), PL 21 (1 specimen, small hydrothermal vent located 150 m from White Lady site in the south-west). Extra specimens from dive PL 10 and PL 20 deep frozen for biochemical analyses. Most specimens come from White Lady vent site (depth 2000 m, 16°59'50"S and 173°55'47"E). Holotype (dive PL 16, 11 July 1989, on White Lady site) deposited in the collections of the Muséum national d'Histoire naturelle, Laboratoire de Biologie des Invertébrés marins et Malacologie (n°UC 350). Paratypes from same dive deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 157044).

Etymology.—The specific name refers to

the peculiar unidentate uncini. The lack of a secondary tooth on the uncini is unique within the family Alvinellidae.

Description.—Holotype 11 mm long and 1.1 mm wide with 81 setigerous segments. Paratypes (14 specimens from PL 16) range from 77 to 88 setigerous segments, with the majority (11 specimens) having from 79 to 83. Length of paratypes ranges from 4.8 mm to 9.2 mm, with an average of 5.2 mm. Color pale grey-pinkish in ethanol, with capillary setae and acicular notopodial hooks yellow; integuments iridescent. Body gradually tapering from about setigerous segment 50 to the end of the body. A medio-ventral row of small shields present.

Prostomium well developed, with ovi-form shield shape, clearly separated from buccal segment by deep grooves, with anterior median incision on two thirds of length; with small glandular notch visible (with SEM) at base of incision. Buccal apparatus, from dorsum to ventrum, with many grooved tentacles in several rows on buccal membrane arising from dorsal side of buccal cavity; length of tentacles highly variable from one individual to the next one, possibly due to preservation. Paired large ventral tentacles and ventral organ absent.

Buccal segment laterally and ventrally visible, well separated from prostomium and from segment II. First visible segment (II) achaetous, laterally and ventrally discernible, clearly separated from peristomium and from branchial region. First 25 to 30 setigerous segments with notopodia only.

Branchial region with four segments, preceded by one reduced asetigerous segment, visible laterally and ventrally (segment II). First branchial segment (segment III) asetigerous, totally fused with two first setigerous segments. Third setigerous segment well separated from others. Following three segments setigerous, with notopodia dorsally elevated in laterodorsal row, with notopodia of same size as those of following segments.

Branchiae four pairs, all similar, arranged as funnel-like structure, with strong basal stem bearing small secondary filaments and thin terminal tip devoid of secondary filaments as long as basal stem. Branchial stem bearing one, sometimes two, bean-shaped vesicles on internal side near base. Secondary filaments inserted along stem on two opposite areas; each leaf-shaped, strongly flattened, with median ciliated area, and pointed tip. These secondary filaments reminiscent of species of *Alvinella*.

Notopodia, from setiger 1 to end of body (7th setiger excepted) each cylindrical, bearing two groups of capillary setae. Notopodia without digitiform lobes. Setiger 7 strongly modified, with slightly reduced cylindrical notopodia, bearing two to three straight short acicular notopodial setae on each side. Setiger 8 not modified.

Cylindrical notopodia and uncinigerous neuropodial tori on each segment from setigerous segment 26 to 29 (with a majority from 28 to 29). Uncini numerous (20 to 50 per torus), in single rows, with teeth directed anteriorly (retrogressive arrangement). Uncini with only a single main tooth, lacking a secondary tooth.

Pygidium rounded, with five conspicuous rounded papillae, two ventral paired papillae and three smaller, dorsal ones.

Tubes unknown.

Ecology.—From observations made on the White Lady hydrothermal site, the alvinellid worms colonize the whitish mass of anhydrite, living close to high temperature (285°C) translucent desalinated hydrothermal fluid openings. On videotapes obtained by the submersible 3 CCD TV camera, the branchial fans of *Paralvinella* spp. are visible at the surface of the mass of anhydrite. The worms belong to *P. unidentata* and to *P. fijiensis*, another species (see below), that are not distinguishable during the sampling procedure.

Discussion.—Since the discovery of the first species of *Paralvinella*, *P. grasslei* Desbruyères & Laubier, 1982, six species or

subspecies have been described within the genus: *P. palmiformis* Desbruyères & Laubier, 1986, *P. pandorae pandorae* Desbruyères & Laubier, 1986, *P. pandorae irlandei* Desbruyères & Laubier, 1986 (Desbruyères & Laubier 1986), *P. dela* Detinova, 1988, *P. hessleri* Desbruyères & Laubier, 1989 (Desbruyères & Laubier 1989) and *P. bactericola* Desbruyères & Laubier 1991 (Desbruyères & Laubier 1991).

Among these species, *P. pandorae* and its two subspecies are clearly distinguished by the presence of uncini from setigerous segments 5 or 6 (depending on the subspecies), a unique situation within alvinellids considered as a plesiomorphous character.

The following morphological features can be used to assess the relationship between species and groups of related species: The total number of segments and its range of variation (primitive situation: 100 to 150 segments, with a large range of individual variation; apomorphous situation, 60 to 80 segments, with a reduced range of individual variation); the rank of occurrence of the anteriormost neuropodial uncinigerous torus (first uncinigerous torus anterior to the modified setigerous segment in plesiomorphous situation, first uncinigerous torus from segment 13 to more than segment 60 in apomorphous situation). The range of variation increases with the rank of occurrence; the buccal apparatus, with two different basic types: the first one bears two large paired lateral tentacles in addition to the small ciliated dorsal tentacles, and a reversible ventral globular organ; the second one lacks the large paired tentacles and has an unpaired pointed organ with a longitudinal slit and a reversible ventral globular organ. The development of the large paired tentacles adapted for different trophic behaviors is considered as an apomorphic feature. *P. unidentata* exhibits a unique buccal structure, reduced to the numerous grooved tentacles inserted on a well developed buccal membrane: this structure basically differs from all previously described species of

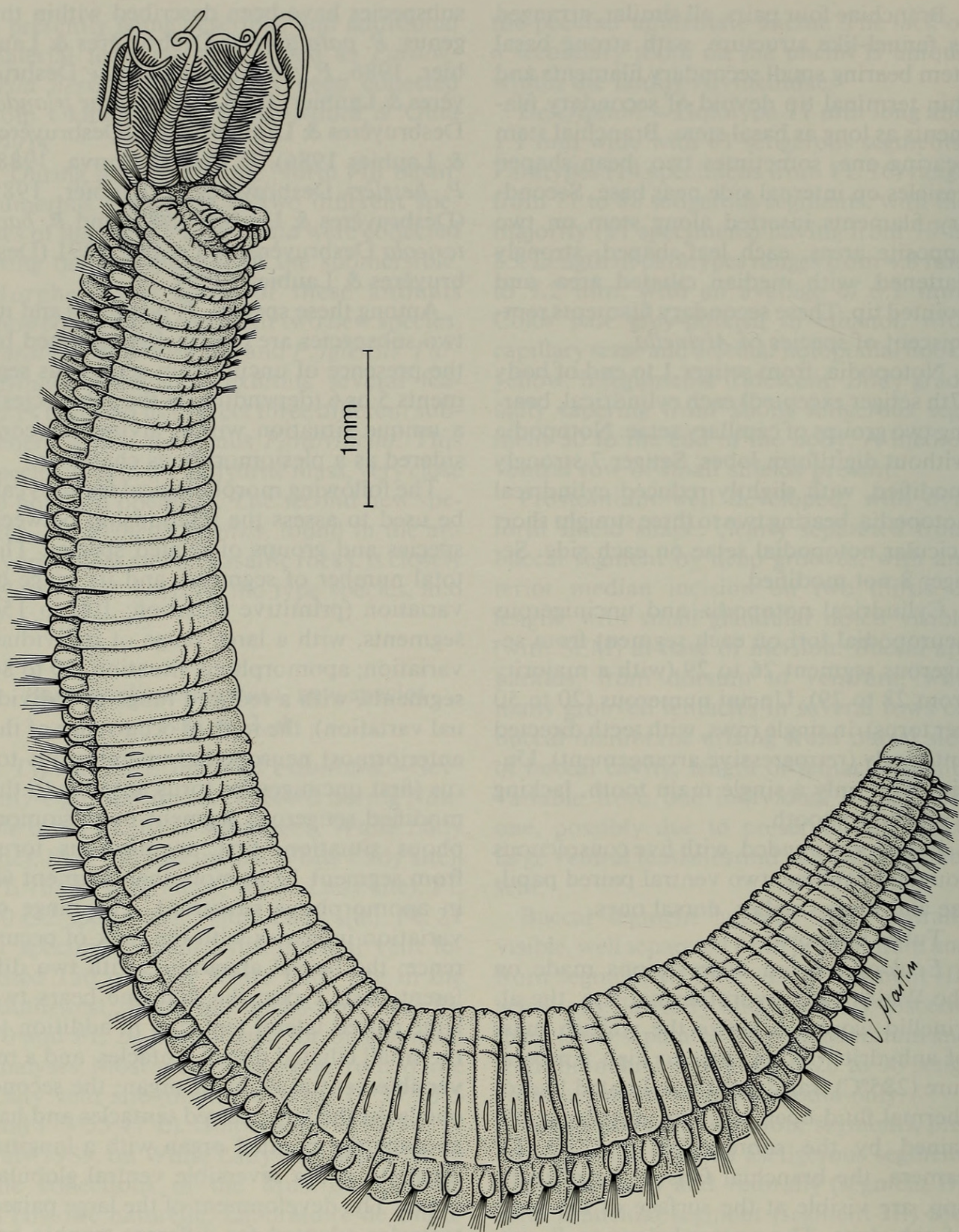


Fig. 1. *Paralvinella unidentata*, new species. Entire animal in ventro-lateral view.

Paralvinella; the shape and position of the secondary filaments of the branchiae. These can be cylindrical and slender or flattened and leaf-shaped, and inserted on two op-

posite or adjacent longitudinal rows. There is no obvious reason to consider either of these structures or situations more primitive than the other one. Nevertheless, con-

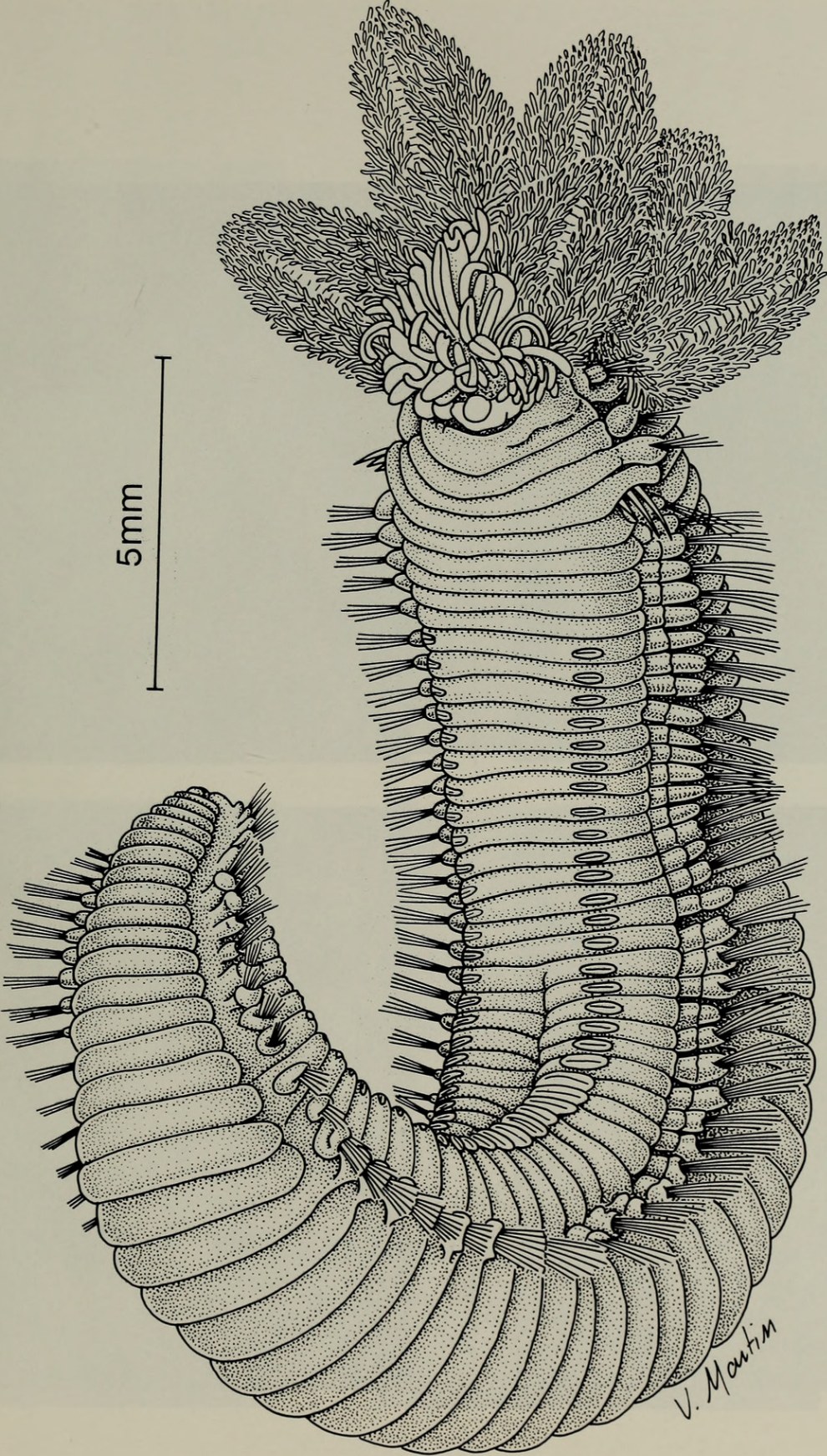


Fig. 2. *Paralvinella fijiensis*, new species. Entire animal in ventro-lateral view.

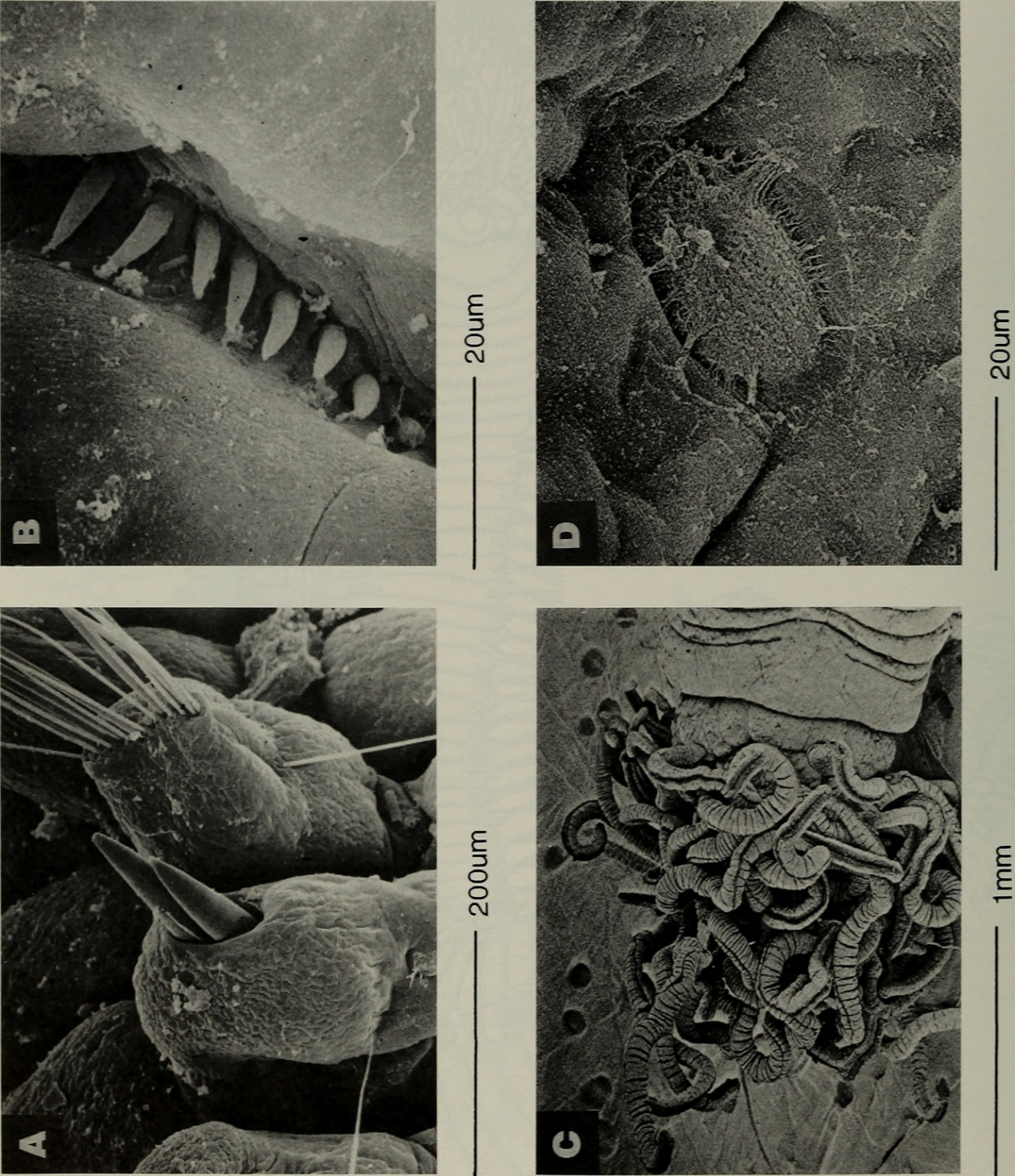
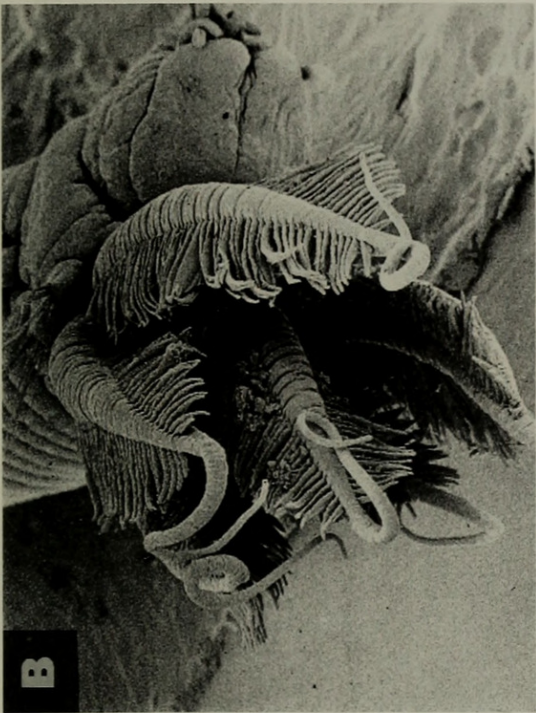
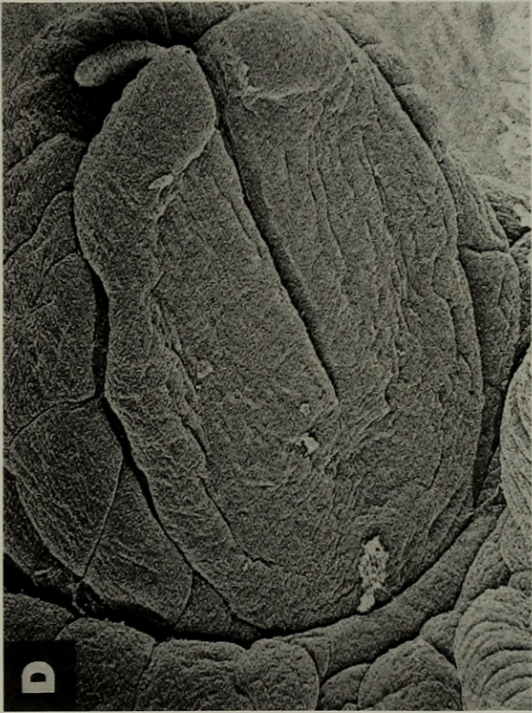


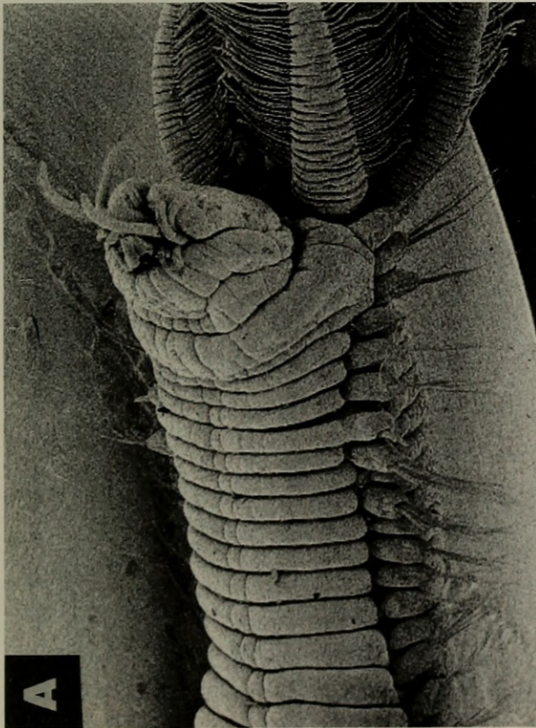
Fig. 3. *Paralvinella unidentata*, new species. A, 7th and 8th parapods, left side of body. B, uncinigerous torus, left side of body. C, anterior part in ventral view, with buccal grooved tentacles extroverted. D, glandular notch at the base of the prostomium.



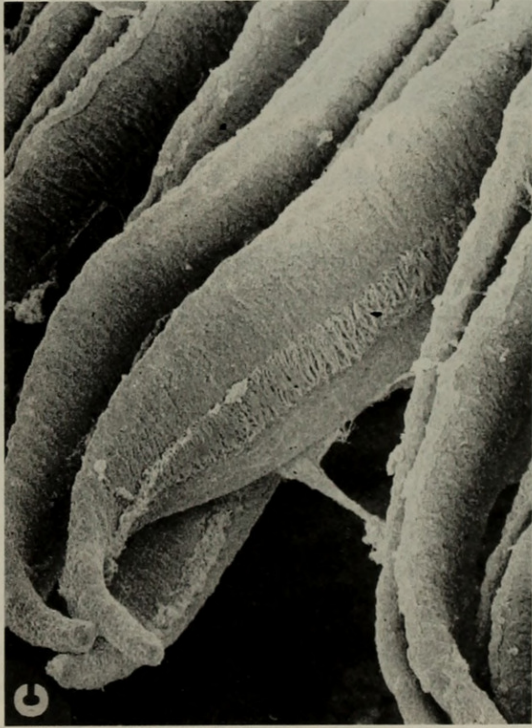
1mm



500um



1mm



100um

Fig. 4. *Paralvinella unidentata*, new species. A, anterior part in ventral view. B, branchial apparatus, showing the terminal tips devoid of secondary filaments. C, leaf-shaped secondary filament, with median ciliated area. D, prostomium in dorso-lateral view, showing the median incision.

sidering the facts that the genus *Alvinella* possesses flattened leaf-shaped secondary filaments and is clearly apomorphic to the genus *Paralvinella* (Desbruyères & Laubier 1986), the question of the systematic rank of *P. unidentata*, with identical flattened leaf-shaped secondary filaments, must be considered carefully; and the shape of the uncini, in all alvinellids but *P. unidentata*, is characterized by one main tooth and one secondary smaller tooth, while in *P. unidentata* there is only one main tooth. Still, the general shape of the uncinus is identical in both groups and the presence or absence of a secondary tooth is not considered an important phylogenetic significance. However, the absence of a secondary tooth can be considered plesiomorphic to the bidentate semiavicular uncini previously known for all alvinellids.

Within the genus *Paralvinella*, *P. unidentata* can be best compared with *P. pandorae* and its two subspecies in the structure of the buccal apparatus and the funnel-like arrangement of the branchiae. However, *P. unidentata* can be easily distinguished by a series of characters including the rank of occurrence and shape of neuropodial uncini and the leaf-shaped secondary filaments of the branchiae.

Paralvinella fijiensis, new species

Figs. 2, 5

Type locality, material examined. — Ninety-five specimens collected and preserved during *Nautila* dives PL 11 (3 specimens, White Lady site), PL 12 (1 specimen, White Lady site), PL 14 (47 specimens; White Lady site), PL 16 (10 specimens, White Lady site), PL 20 (34 specimens, White Lady site). All specimens come from White Lady vent site (depth 2000 m, 16°59'50"S and 173°55'47"E). Holotype (dive PL 14) deposited in the collections of the Muséum national d'Histoire naturelle, Laboratoire de Biologie des Invertébrés marins et Malacologie (n°UC 439). Para-

types from same dive deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM 157043).

Etymology. — The species is named for its geographic origin.

Description. — Holotype 24 mm long and 5 mm wide with 63 setigerous segments. Paratypes (15 specimens from PL 14) range from 50 to 68 setigerous segments. Color pale grey-pinkish in ethanol, with capillary setae and acicular notopodial hooks yellow; integument iridescent. Body maggot-shaped in large specimens; small animals with body gradually tapering posteriorly; medioventral area slightly depressed. When viewed under scanning microscope, integument of intersegmental areas densely covered with small circular glandular areas and secretions from same.

Prostomium reduced medially with two anterior lobes and two nuchal grooves obliquely situated near base. Prostomium laterally separated from lateral parts of buccal segment. Buccal segment laterally and ventrally visible, well separated from prostomium and segment II. Buccal apparatus comprising many grooved tentacles inserted dorsally and two large paired grooved tentacles inserted ventrally, ending with three unequally developed rounded lobes. Edge of main lobe provided with several rows of small rounded internal papillae.

Branchial region comprised of four segments, preceded by one reduced asetigerous segment still visible laterally and ventrally (segment II). First branchial segment asetigerous, ventrally visible. Next three branchial segments (setigerous segments 1 to 3) totally fused. Notopodia of first setigerous segment very reduced; notopodia of 2nd setigerous segment reduced; notopodia of 3rd setigerous segment similar to the following notopodia. Notopodia of setigers 1 to 3 adjacent to stem of external pair of branchiae. Fourth setigerous segment fused ventrally to fourth branchial segment.

Branchiae four pairs, all similar, with a

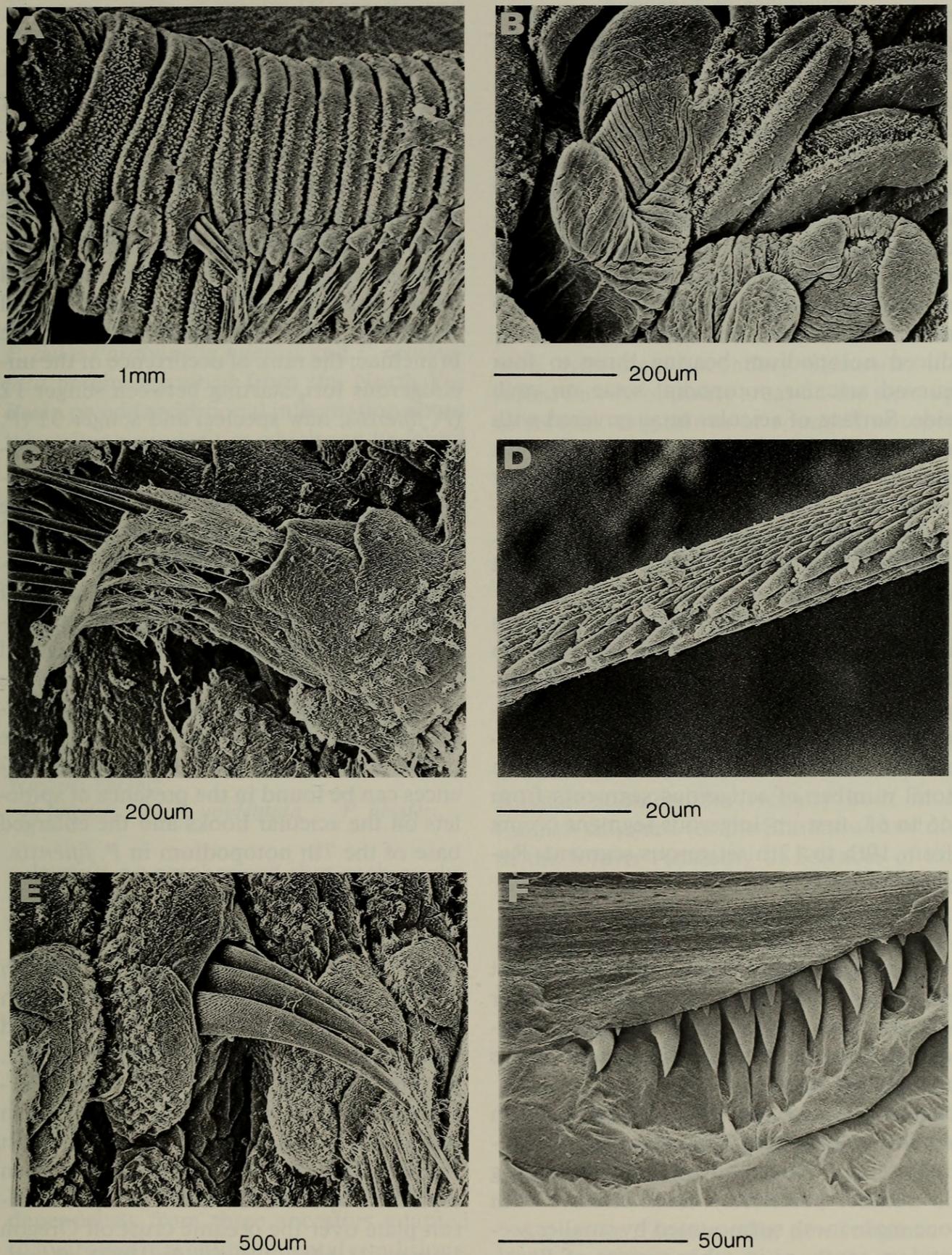


Fig. 5. *Paralvinella fijiensis*, new species. A, anterior part in lateral view. B, buccal apparatus, showing grooved tentacles (right) and the terminal lobes of one of the ventral large tentacles (left). C, left parapod from anterior setiger, showing dorsal lobe. D, capillary seta covered with small spines and two rows of larger ones on the edge. E, modified notopodium of setiger 7, with large acicular hooks. F, uncinigerous torus, right side of body.

strong basal stem. Secondary filaments very abundant, inserted on two opposite areas of stem to end of branchia, reminiscent of *Paralvinella grasslei* and *P. palmiformis*.

Notopodia, from setiger 4 to the end of body (7th setiger excepted) cylindrical, bearing two groups of capillary setae heavily coated with filamentous bacteria. Notopodia from about setiger 9 to setiger 30 bearing dorsal and ventral rounded lobes. Setiger 7 strongly modified, with two reduced dorsal and ventral lobes surrounding a very reduced notopodium bearing three to four curved acicular notopodial setae on each side. Surface of acicular setae covered with minute spinelets; these are longer on convex side of acicular hooks when viewed under SEM. This structure similar to ornamentation of notopodial setae in other segments. Notopodia of setiger 8 with anterior part enlarged.

Uncinigerous neuropodial tori present on each segment from setiger 12 to 19 (13 on the holotype). Occurrence of first uncinigerous torus appears to be inversely proportional to total number of setigerous segments: on a total of 23 individuals, with total number of setigerous segments from 46 to 68, first uncinigerous segment occurs from 19th to 12th setigerous segment. Regression curve:

$$R_o = (96 - N)/2.54$$

where R_o = rank of occurrence of the first uncinigerous torus and N = total number of setigerous segments of the body, indicating that the anteriormost uncinigerous tori appear latest.

Uncini numerous (20 to 50 per row) in single rows, with teeth facing anteriorly (retrogressive arrangement). Uncini increasing in number posteriorly. Each uncinus with one main tooth surmounted by smaller secondary tooth, as in other species of *Paralvinella* (except *P. unidentata*, see above).

Pygidium blunt, without conspicuous papillae.

Ecology.—Most specimens were collected in anhydrite samples together with *P. unidentata*; on one occasion, a tube inhabited by *P. fijiensis* was found on a piece of basalt.

Discussion.—Within the genus *Paralvinella*, *P. fijiensis* exhibits clear relationships with the stem species *P. grasslei* and its close relative *P. palmiformis*. These three species have in common: the structure of the buccal apparatus, with two large trilobate paired ventral tentacles; the general shape of the branchiae; the rank of occurrence of the uncinigerous tori, starting between setiger 12 (*P. fijiensis*, new species) and setiger 31 (*P. palmiformis*); and the first setigerous segment is very reduced, and the second setigerous segment reduced, emphasizing the importance of the cephalization processes.

Within this group of three species, *P. fijiensis* is characterized by the number of setigerous segments (maximum 68 in *P. fijiensis*, compared to 110 in *P. grasslei* and 118 in *P. palmiformis*), the small papillae of the main end of the trilobate paired buccal tentacles and the shape and relative size of the prostomium. Additional minor differences can be found in the presence of spinelets on the acicular hooks and the enlarged base of the 7th notopodium in *P. fijiensis*.

Conclusion

All *Paralvinella* species except *P. hessleri* and the two new species described herein are known from the East Pacific Rise and related ridge systems in the Eastern Pacific. Within this general framework, two different species groups can be distinguished in the Northern and Southern parts of the East Pacific ridge system. These parts have been separated by the subduction of the American plate over the oceanic crust off Oregon starting 35 MY (Tunnicliffe 1988). *P. palmiformis* and *P. pandorae pandorae* live in the Northern part, while *P. grasslei* and *P. pandorae irlandei* live in the Southern part.

These two pairs of species (*P. grasslei* and *P. palmiformis*) or subspecies (*P. p. irlandei* and *P. p. pandorae*) have been regarded as examples of sibling species (Desbruyères & Laubier 1986). Two additional species, *P. bactericola* in the Southern area and *P. dela* in the Northern one, have been discovered, providing a third example of a closely related paired species. More recently, *P. hessleri*, collected in the Mariana back-arc Basin in the Western Pacific, was found to exhibit a close relationship with *P. bactericola* and *P. dela*. *Paralvinella fijiensis* and *P. unidentata* herein described from the North Fiji Basin provide additional information about the striking similarities which can be found between the different groups of species living in these three major areas:

Evolutionary groups:

Group 1	Group 2	Group 3
East Pacific Rise:		
<i>P. grasslei</i>	<i>P. p. irlandei</i>	<i>P. bactericola</i>
Juan de Fuca-Explorer:		
<i>P. palmiformis</i>	<i>P. p. pandorae</i>	<i>P. dela</i>
Western Pacific:		
<i>P. fijiensis</i>	<i>P. unidentata</i>	<i>P. hessleri</i>

It must be emphasized that each evolutionary group within the genus *Paralvinella* is present in each of the three geographic areas. Moreover, morphological differentiation is not related to the distance between the hydrothermal areas: the three species from the Western Pacific are much more different from one another than they are from related species in other biogeographical areas.

We hypothesize that these three different groups of *Paralvinella* species evolved independently from three ancestors adapted to hydrothermal environmental conditions. As a consequence of this hypothesis, we propose the establishment of three subgenera, that can be diagnosed as follows:

Subgenus *Paralvinella*

Type species. — *Paralvinella (Paralvinella) grasslei* Desbruyères & Laubier, 1982

Other species. — *P. (P.) palmiformis* Desbruyères & Laubier, 1986 and *P. (P.) fijiensis*

Diagnosis. — Buccal apparatus, comprising, from dorsum to ventrum, numerous buccal grooved retractile tentacles inserted on a semi-circular buccal membrane, two large paired trilobate appendages and a globular eversible ventral organ. Branchiae with cylindrical secondary filaments, inserted on two opposite areas on the stem up to its end. Digitiform or rounded notopodial lobes present on some anterior setigerous segments.

Subgenus *Miralvinella*, new subgenus

Type species. — *Paralvinella (Miralvinella) dela* Detinova, 1988

Other species. — *P. (M.) hessleri* Desbruyères & Laubier, 1989 and *P. (M.) bactericola* Desbruyères & Laubier, 1991.

Etymology. — *Miralvinella*, from *Alvinella* and MIR, the name of the two deep-sea Russian submersibles recently built in a Finnish shipyard for the Shirshov Institute of the former Academy of Sciences of the Soviet Union.

Diagnosis. — Buccal apparatus complex, comprising from dorsum to ventrum numerous grooved tentacles inserted on a buccal membrane, two large deeply grooved tapering paired tentacles and a globular eversible ventral organ. Branchiae with cylindrical secondary filaments, inserted on two opposite areas on the stem up to its end. Digitiform notopodial lobes present on some anterior segments.

Subgenus *Nautalvinella*, new subgenus

Type species. — *Paralvinella (Nautalvinella) pandorae* Desbruyères & Laubier, 1986

Other species. — *P. (N.) unidentata*

Etymology.—*Nautalvinella*, from *Alvinella* and *Nautile*, the French deep-sea submersible of IFREMER which was used during the STARMER cruise and previous expeditions on hydrothermal vents areas.

Diagnosis.—Buccal apparatus comprising numerous grooved tentacles inserted dorsally on a buccal membrane. A median hollowed pointed lobe can be present in some species. No large paired ventral tentacles. No ventral organ. Branchiae with numerous leaf-shaped secondary filaments inserted on two more or less adjacent lines on the stem. Terminal part of the stem devoid of secondary filaments. No digitiform notopodial lobes.

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